

Tamias quadrivittatus. By Troy L. Best, Stephanie L. Burt, and Jarel L. Bartig

Published 2 June 1994 by The American Society of Mammalogists

Tamias quadrivittatus (Say, 1823)

Colorado Chipmunk

Sciurus quadrivittatus Say, 1823:45. Type locality not given, but was in the Arkansas River Valley in the vicinity of Pike's Peak, Colorado. Later restricted to Arkansas River, about 26 miles below Canyon City [Pueblo Co.—Ellerman, 1940:433], Colorado (Merriam, 1905:163).

Tamias quadrivittatus: Bachman, 1839:74. First use of name combination.

Eutamias hopiensis Merriam, 1905:165. Type locality "Kear Canyon, Painted Desert [Navajo Co.—Ellerman, 1940:433], Arizona."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains 25 species (Wilson and Reeder, 1993). *T. quadrivittatus* (Fig. 1) is in the subgenus *Neotamias* (Levenson et al., 1985) and the *quadrivittatus* species complex, which includes *T. canipes*, *T. cinereicollis*, *T. quadrivittatus*, and *T. rufus* (Patterson, 1984b). Two subspecies of *T. quadrivittatus* are recognized (Patterson, 1984a):

T. q. australis (Patterson, 1980:460). Type locality "3.5 mi S, 1.5 mi E Organ, 6800', North fork Pine Tree Trail, Aguirre Springs, T22S R4E Sec. 30, Doña Ana Co., New Mexico."

T. q. quadrivittatus Say, 1823:45, see above (*animosus* Warren, *gracilis* J. A. Allen, and *hopiensis* Merriam are synonyms).

DIAGNOSIS. *Tamias quadrivittatus* is sympatric or parapatric with *T. dorsalis*, *T. minimus*, *T. umbrinus* (Callahan, 1976), and *T. rufus* (Patterson, 1984a). The skull of *T. quadrivittatus* (Fig. 2) is larger than that of any other chipmunk within its range (Howell, 1929).

Compared with *T. minimus*, *T. quadrivittatus* has bright orange on the shoulders. In addition, *T. quadrivittatus* has three prominent dark dorsal stripes while *T. minimus* has five (Hoffmeister, 1986). The ears and hind feet of *T. minimus* are smaller (Howell, 1929). Where *T. quadrivittatus* and *T. minimus* occur together, *T. quadrivittatus* is recognized by its larger size and affinity for rocky sites instead of wooded habitats. The elevational range of *T. quadrivittatus* on the eastern slope of the Rocky Mountains is more restricted than that of *T. minimus* (Armstrong, 1972).

Tamias quadrivittatus and *T. rufus* are narrowly allopatric or parapatric in western Colorado and northern Arizona. Although their sympatric occurrence has not been demonstrated, the two approach one another in the Gunnison River Valley, Colorado (Patterson, 1984a). *T. rufus* differs from *T. quadrivittatus* as follows: smaller, especially in length of hind foot and total length; skull shorter, but not especially narrower except in interorbital region; auditory bullae relatively longer; nasals shorter. Color is variable, but *T. rufus* usually is paler and redder, with less black in the dark dorsal stripes (Hoffmeister, 1986; Hoffmeister and Ellis, 1979). Although *T. quadrivittatus* averages larger in cranial characters than *T. rufus*, especially in southwestern populations, extensive overlap exists. Despite this broad overlap, average size differences are statistically significant in most cranial characters. In areas of juxtaposition, *T. quadrivittatus* and *T. rufus* show no evidence of intergradation in bacular morphology. Bacula of *T. quadrivittatus* average larger in all dimensions than those of *T. rufus*. There is no overlap in total length, and length of tip shows limited overlap (the shortest *T. quadrivittatus* was 1.25 mm compared with 1.32 mm for the longest *T. rufus*). Baubella of *T. quadrivittatus* (average length of tip, 0.838 mm) are larger than baubella of *T. rufus* (average length of tip, 0.706 mm—Patterson, 1984a).

Compared with *T. umbrinus*, the jugal bone of *T. quadrivittatus* is broad in lateral aspect and flares dorsally (average width is 2.0

mm; range, 1.7–2.4). In *T. umbrinus*, the bone typically is narrower (average width is 1.5 mm; range, 1.2–1.8) and the entire zygomatic arch is lighter and more slender. The skull of *T. quadrivittatus* is relatively shorter and broader than that of *T. umbrinus*. The average ratio of zygomatic breadth to greatest length of skull in *T. quadrivittatus* is 0.547 (range, 0.535–0.569). In a sample of *T. umbrinus*, the average ratio is 0.536 (range, 0.524–0.548). Absolute differences between these ratios are small, but cranial differences that the ratios reflect are visible to the unaided eye. *T. quadrivittatus* has a less elongate braincase than *T. umbrinus* (Armstrong, 1972). The basic color of *T. quadrivittatus* is orange and it is brown in *T. umbrinus*. Coloration is especially different on the sides and shoulders. On the anterior part of the forehead, *T. quadrivittatus* is orange to buffy while *T. umbrinus* is pale gray in Arizona (Hoffmeister, 1986), but in Colorado the forehead of *T. quadrivittatus* is gray and that of *T. umbrinus* is brown (B. J. Bergstrom, in litt.). These species differ in one to several allozymes, depending upon where in the range they are sampled (Bergstrom and Hoffmann, 1991; Levenson et al., 1985). Where the geographic ranges of *T. quadrivittatus* and *T. umbrinus* approach each other, *T. umbrinus* occupies life zones at higher elevation. Wherever either one of these species occurs alone on a mountain, it occupies both the higher and lower life zones (White, 1953a).

Tamias canipes, *T. cinereicollis*, and *T. quadrivittatus* are similar in morphology and habitat. Of the three, *T. quadrivittatus* is the smallest, most brightly colored, and brownest, and especially on the dorsum of the tail (Findley et al., 1975; Patterson, 1980). Compared with *T. cinereicollis*, *T. quadrivittatus* averages smaller for palatilar length and postorbital breadth and is orange on the shoulders rather than gray (Hoffmeister, 1986). Compared with *T. canipes*, *T. quadrivittatus* lacks the gray on the dorsal surface of the hind foot (Findley et al., 1975). Karyotypically, *T. quadrivittatus* exhibits the type B karyotype of *Tamias* while *T. canipes*, *T. cinereicollis*, and *T. durangae* exhibit type A karyotypes. Bacula of *T. quadrivittatus* are intermediate to the rest of the species complex, being shorter than *T. cinereicollis*, shorter and less robust than *T. durangae*, and longer and less robust than *T. canipes*. Generally, cranial dimensions of *T. quadrivittatus* are smaller than those of geographically adjacent taxa (Patterson, 1980).

GENERAL CHARACTERS. *Tamias quadrivittatus* is medium-sized for the genus. In summer pelage (June–September), the head is cinnamon and shades on the crown to pale drab or smoke gray. The stripe through the eye is fuscous black and bordered with



FIG. 1. A male *Tamias quadrivittatus australis* at Aguirre Springs, Doña Ana Co., New Mexico. Photograph by T. L. Best.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias q. quadrivittatus* from Gordon Creek near junction of Piedra River, Archuleta Co., Colorado (female, University of New Mexico Museum of Southwestern Biology 10077). Greatest length of cranium is 36.2 mm. Photographs by T. H. Henry.

cinnamon. Other facial stripes are rather narrow and mixed with cinnamon and fuscous. The sides of the nose and sometimes of the face are washed with clay color. The ears are fuscous or fuscous black and edged on the anterior margin with ochraceous tawny and broadly margined posteriorly with grayish white; postauricular patches are grayish white. The dark dorsal stripes are black and margined with ochraceous tawny; the outer pair may be mostly tawny. The lateral stripe is fuscous, fuscous black, or tawny. The pale dorsal stripes are grayish white; the outer pair usually is creamy white. The sides are ochraceous tawny and shade on the shoulders to cinnamon. The rump and thighs are cinnamon buff mixed with smoke gray. The front feet are cinnamon buff and the hind feet are pinkish buff or pinkish cinnamon. Dorsally, the tail is fuscous black (bases of the hairs are cinnamon) and overlaid with pinkish buff. Ventrally, the tail is ochraceous tawny or tawny, bordered with fuscous black, and edged with pinkish buff; underparts are creamy white. In winter pelage (October–December), coloration is similar to summer pelage,

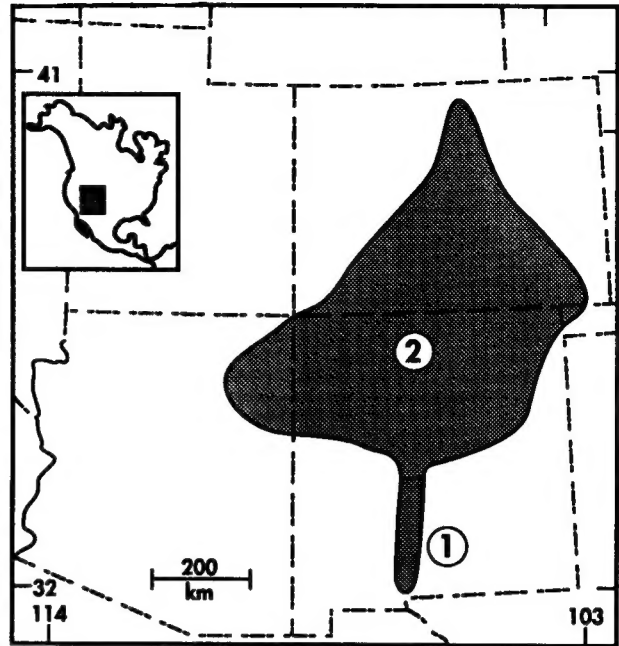


FIG. 3. Distribution of *Tamias quadrivittatus* in western North America (Armstrong, 1972; Patterson, 1984a): 1, *T. q. australis*; 2, *T. q. quadrivittatus*.

but the median pair of pale dorsal stripes is more grayish (color nomenclature follows Ridgway, 1912—Howell, 1929).

Average body mass of *T. q. quadrivittatus* in Colorado is 59.6 g (range, 45.2–69.8—Sutton, 1953). Average measurements (in mm) of *T. q. australis* and *T. q. quadrivittatus*, respectively, are: total length, 211.5, 220.8; length of tail, 91.5, 99.6; length of hind foot, 32.0, 32.9; length of ear, 20.5, 18.7; greatest length of cranium, 35.5, 35.6; zygomatic breadth, 19.5, 19.4; breadth of cranium, 15.0, 14.9; length of mandible, 20.1, 20.5; nasal length, 10.8, 10.3; length of molar toothrow, 5.5, 5.6; interorbital breadth, 7.9, 8.1; nasal width, 3.2, 2.8; diagonal length of orbit, 9.5, 9.4; length of premaxilla, 11.8, 11.1; depth of cranium, 14.2, 14.3; body mass (in g), 57.2, 57.6 (Patterson, 1980).

Overall, females average larger than males. However, the only individual characters showing significant differences between genders are palatal length (Hoffmeister, 1986) and length of head and body (average: males, 125.3; females, 132.0—Levenson, 1990).

The baculum reaches adult size prior to complete dental emergence (Patterson, 1984a). The baculum has a thick shaft, the keel is proportionally low and 25% of the length of the tip, the tip is 30–44% of the length of the shaft, the angle formed by the tip and shaft is 130°, the distal 33% of the shaft is compressed laterally (White, 1953b), and the base is not markedly wide (Hoffmeister, 1986). There is extensive geographic variation in characters of the baculum. Average and range of means of measurements of bacula (in mm) for nine populations of *T. quadrivittatus* are: total length, 4.45 (4.20–4.74); length of tip, 1.39 (1.32–1.51); height of keel, 0.50 (0.47–0.57); width of tip, 0.45 (0.38–0.52); width of neck, 0.27 (0.25–0.32); width of base, 0.74 (0.68–0.82); bend of shaft, 0.63 (0.57–0.72); angle of tip, 128° (124–132—Patterson, 1984a). Average measurements (in mm) of bacula of *T. q. australis* from the Organ Mountains, New Mexico, and *T. q. quadrivittatus* from the Sandia and Manzano mountains, New Mexico, respectively, are: total length, 4.46, 4.46; length of tip, 1.37, 1.40; height of keel, 0.53, 0.48; bend of shaft, 0.64, 0.57; width of base, 0.76, 0.68; width of neck, 0.30, 0.25; width of tip, 0.47, 0.47; angle of tip, 126.94°, 128.19° (Patterson, 1980).

DISTRIBUTION. *Tamias quadrivittatus* occurs in the transition and Canadian life zones (Howell, 1929) of northeastern Arizona, central and southern Colorado, and northern and central New Mexico (Fig. 3; Patterson, 1984a). The Colorado chipmunk occurs at elevations from 1,380 to 3,360 m (Bergstrom and Hoffmann, 1991; Howell, 1929; Sutton, 1953).

FOSSIL RECORD. The only known fossil of *T. quadrivittatus* is from Pleistocene deposits in northwestern Oklahoma (Dalquest and Stangl, 1989). *T. q. australis* diverged from *T. q. quadrivittatus* (Patterson, 1980). Using allozyme data, the divergence time between *T. quadrivittatus* and *T. umbrinus* was 1,145,000 years ago. Divergence time between *T. quadrivittatus* and *T. minimus* was 854,000 years ago (Sullivan, 1985).

FORM AND FUNCTION. In Arizona, the Colorado chipmunk apparently molts from winter pelage in May–July with a second molt in autumn (Hoffmeister, 1986). An adult male from Boulder, Colorado, showed new summer pelage coming in irregularly over the anterior back on 11 June. An adult female from Copperton, Cibola Co., New Mexico, was still in winter pelage on 13 July; new pelage was beginning to appear in the middle of the back (Howell, 1929).

As in all members of the subgenus *Neotamias*, the dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22 (Hoffmeister, 1986; Howell, 1929). Length of maxillary toothrow seems to decrease with age in adults (Long and Cronkite, 1970). Colorado chipmunks in which replacement of P3 and P4 have reached occlusal level are adults, whereas those with a fully erupted M3 and deciduous premolars are subadults (Patterson, 1984a). Subadults with a deciduous P4 fully erupted can be distinguished from adults by the presence of a small hole in the bone lingual to this tooth. This is not found in adults. Also, the anterior root of P4 is more slanted in subadults than adults (Hoffmeister, 1986).

The total volume of blood in a 50-g Colorado chipmunk was ca. 3 cm³. Animals that lose ca. 20–30% of their blood often go into shock, but usually recover within 8 h (Rigg, 1965a). There is daily variation in the time it takes for blood to clot (Everson, 1960; Rigg, 1967). *T. quadrivittatus* has coagulation times that are shorter when it is active and prolonged when it is inactive. The average time for the conversion of prothrombinogen to prothrombin is 10.5 s (Rigg, 1967). Amounts of prothrombin, proaccelerin, proconvertin, and prothrombinogen do not vary over a 24-h period as does the clotting time (Rigg, 1965b).

Average daily intake of water is ca. 10–20 cm³/day. *T. quadrivittatus* drinks nearly as little as the Ord kangaroo rat (*Dipodomys ordii*) and northern grasshopper mouse (*Onychomys leucogaster*), both arid-habitat species (Boice, 1968; Boice and Boice, 1968). At a body mass of 68 g, minimum water requirement during hibernation is 5.9% of body mass/day (Blake, 1977).

Tamias quadrivittatus can be anesthetized with 0.15 cm³ of sodium diethylbarbiturate. Hair can be removed with the common depilatory agent, calcium thioglycollate (Rigg, 1965a).

ONTOGENY AND REPRODUCTION. During the breeding season, most *T. quadrivittatus* are in male-female pairs (Hooper, 1941). Reproductive activity of *T. q. australis* appears to be bimodal, i.e., February and July, coinciding with periods of reduced water stress and increased primary productivity. However, throughout much of its range, *T. q. quadrivittatus* breeds in late spring. Thus, *T. q. australis* and *T. q. quadrivittatus* appear to differ in the timing of their reproductive cycles (Patterson, 1980).

In Colorado, three females had five fetuses each on 10–20 May (Warren, 1942). In New Mexico, most litters are born from early May (Bailey, 1931) to early June. In northwestern New Mexico, 11 of 17 females were lactating and four were pregnant 1–16 June; the number of embryos were two, three, four, and four, and they were 20–30 mm long (Hooper, 1941). There are eight mammae; one pair inguinal, two pair abdominal, and one pair pectoral (Bailey, 1931).

One litter of two to six young is raised each year. Young are almost full-grown by July and August, but small young may be present in early October. Presence of young in October may indicate that two litters are produced each year (Bailey, 1931), as does the presence of males with scrotal testes and pregnant females in July, and lactating females in September (Bergstrom, 1986). Many half-grown young actively gather food by mid-June. Stomachs of small or nearly half-grown young may contain a mixture of milk and other foods such as green seeds, vegetation, or berries (Bailey, 1931).

ECOLOGY. The Colorado chipmunk occupies a variety of habitats, including: desert scrub, 9% of habitats occupied; grassland-chaparral, 9%; woodland, 36%; mixed conifer, 28%; spruce-fir (*Picea*, *Abies*, *Pseudotsuga*), 17%; alpine tundra, 1% (Lomolino et

al., 1989). Many populations are restricted to mountain ranges that are surrounded at lower elevations by grassland or desert biomes. Each of these montane populations now is a genetically isolated unit. The isolation of these montane populations can be dated to the withdrawal of the Wisconsin ice-sheet ca. 10,000 years ago (Patterson, 1981). In Arizona, *T. q. quadrivittatus* is found in association with pinyon pine (*Pinus*), juniper (*Juniperus*), and rocks (Hoffmeister, 1986).

In Colorado, *T. q. quadrivittatus* occurs in a variety of habitats, e.g., pinyon-juniper forests, spruce-fir forests, and open, rocky, brushy areas (Lechleitner, 1969). It occurs at all elevations where conifers are found, and is more closely associated with conifers than other types of vegetation. Concentrations of *T. q. quadrivittatus* principally are around forest margins rather than in dense stands of trees. It is found in rocky areas, streamside thickets, and in places where rotting logs, stumps, and brush are abundant. The Colorado chipmunk often is found far away from a constant source of water (Sutton, 1953). In Las Animas Co., it occurs on sandstone mesas with gulches, shallow canyons, and scattered pinyon and juniper trees at elevations $\geq 1,500$ m. This area of Colorado is dry with few running streams, springs, or water holes (Warren, 1909). In north-central Colorado, percent frequencies of the most common trees in habitats occupied by *T. q. quadrivittatus* are: Ponderosa pine (*Pinus ponderosa*), 48.4; Douglas fir (*Pseudotsuga menziesii*), 25.6; Rocky Mountain juniper (*Juniperus scopulorum*), 21.3; quaking aspen (*Populus tremuloides*), 2.8. Similar data for the most common species of shrubs are: currant-gooseberry (*Ribes*), 24.1; antelope-brush (*Purshia tridentata*), 12.1; bramble (*Rubus*), 11.6; mountain mahogany (*Cercocarpus montanus*), 8.7; chokecherry (*Prunus virginiana*), 8.4; cliff-bush (*Jamesia americana*), 7.6; fragrant sumac (*Rhus trilobata*), 4.3 (Bergstrom, 1986).

In New Mexico, the range of *T. q. quadrivittatus* is largely coincident with the Ponderosa pine zone of the mountains of northern New Mexico, generally at elevations of 2,250–2,550 m. Occasionally, Colorado chipmunks are above this zone on warm slopes. Along the Canadian River near the lower edge of the upper Sonoran life zone, *T. quadrivittatus* occurs across the river from mesquites (*Prosopis*). However, it lives in dense thickets on steep, cold slopes where conditions are similar to those 300 m higher on warmer slopes. Generally, *T. quadrivittatus* is found throughout Ponderosa pine forests, but is not restricted to forest cover. Colorado chipmunks occur in habitats with brushy and rocky slopes, scrub-oak (*Quercus*) gulches, old burns, berry patches, and thickets of second growth, or any combination of these that affords food and cover (Bailey, 1931). Some Colorado chipmunks are found in spruce-fir areas, but *T. minimus* usually is the most common chipmunk there. At low elevations, in scattered pinyon-juniper woodland, *T. quadrivittatus* may be common, especially if rock outcrops are available (Findley et al., 1975). *T. q. australis* is most abundant in the broad dissected basin of Aguirre Springs, Doña Ana Co. (Fig. 4). This north-facing basin supports some Ponderosa pine and deciduous oaks. Many Colorado chipmunks also occur here in scrub oak-juniper habitats. One occurred in a wash containing Apache plume (*Fallugia*) and sumac (*Rhus*—Patterson, 1980).

Tamias q. quadrivittatus is most common in pinyon-juniper habitat in the Black Mesa region of Oklahoma. Except for sparse clumps of bluestem (*Andropogon*), the slopes primarily consist of rocks and scattered pinyon pines and junipers. The rocks commonly are large and flat, forming long ledges, crevices, and much exposed area (Geluso, 1970).

Tamias quadrivittatus is omnivorous (Bailey, 1931). It eats seeds or fruits of shrubby cinquefoil (*Potentilla*), serviceberry (*Aamelanchier*), honeysuckle (*Lonicera*), Canadian thistle (*Carduus*), currant-gooseberry (*Ribes*), chokecherry (*Prunus*), snowberry (*Symphoricarpos*), elderberry (*Sambucus*), golden pea (*Thermopsis*), lupine (*Lupinus*), rose (*Rosa*), dandelion (*Taraxacum*), globeflower (*Trollius*), sedge (*Carex*), and sumac (*Rhus*—Sutton, 1953). *T. quadrivittatus* also eats pollen, buds, and cones of Ponderosa pine, buds of Douglas fir, Rocky Mountain juniper, cliff-bush, currant-gooseberry, maple (*Acer glabrum*), mountain mahogany, chokecherry, antelope-brush, fruits of shrubs, yarrow (*Achillea*), fungi (Erdogonaceae, Hydnoraceae, Hysterangiaceae, Tuberaceae), arthropods (adults and larvae of Lepidoptera), composites, herbs, and grasses (Bergstrom, 1986). Other foods include acorns (*Quercus*—Bailey, 1931; Warren, 1942), seeds of maple trees (*Acer*—Bailey, 1931), Douglas fir, grasses (Tomberlin, 1968), forbs, and mountain ma-



FIG. 4. Habitat occupied by *Tamias quadrivittatus australis* near Aguirre Springs, Doña Ana Co., New Mexico. Photograph by T. L. Best.

hogany (*Cercocarpus parvifolius*), fruits of prickly pear cacti (*Opuntia*), juniper berries, wild cherries (*Prunus*), and June berries (*Ame-lanchier*—Cary, 1911). *T. quadrivittatus* may occur in large numbers around old stacks of millet from which it can carry away seeds (Sutton, 1953). It also supplements its diet with picnic scraps and has been observed to eat seeds at the top of spruce trees (Rigg, 1965a). In northern Colorado, seeds of ninebark (*Physocarpus monogynus*) was the most abundant material in the feces of *T. quadrivittatus* (Bergstrom, 1986).

In captivity, *T. quadrivittatus* will eat whole oats and sunflower seeds (Rigg, 1965a), and can be maintained on Purina Lab Chow (Rigg, 1967). The Colorado chipmunk can be captured in Sherman live traps that have been provided with cotton nesting material and baited with peanut butter, scratch grain, or sunflower seeds (Bailey, 1931; Bergstrom, 1988; Rigg, 1967).

In Colorado, the juvenile to adult ratio was 1:1, with a highly uneven sex ratio. The average movement was 95 m (range, 3–279 m), and all movements were confined to Ponderosa pine habitat (Tomberlin, 1968). Average size of home range (determined using radiotransmitters weighing ca. 3 g) is 2.7–2.8 ha; this does not differ from home ranges of *T. minimus* or *T. umbrinus* (Bergstrom, 1988). Rate of overwinter survival is <33%, and local population extinction or near-extinction is a common occurrence (Bergstrom and Hoffmann, 1991).

In Colorado, *T. quadrivittatus* often is associated with *T. minimus*, which usually is more abundant (Warren, 1942). *T. quadrivittatus* appears more ecologically restricted than *T. minimus*, but five habitat types occur within the 400-m elevational range of *T. quadrivittatus* and it inhabits four of them (Bergstrom and Hoffmann, 1991). *T. quadrivittatus* shows a preference for rocky sites, whereas *T. minimus* occupies low-gradient sites with open, grassy habitats or meadows (Bergstrom, 1986). In southern Colorado, *T. quadrivittatus* occurs at high and low elevations, but where it approaches the range of *T. umbrinus*, *T. quadrivittatus* occupies the

pinyon-juniper habitat of lowlands. *T. umbrinus* occupies only talus-slide habitat margined by spruce and fir in the highest elevations of northern and central Colorado (Long and Cronkite, 1970). Each species occupies a much greater elevational range in regions where the other is absent (Armstrong, 1972). In the Front Range of the Rocky Mountains, the 2,130-m contour line is a good predictor of parapatry between *T. quadrivittatus* and *T. umbrinus* along elevational transects. At three sites, these species were captured <100 m from each other and at one site they overlapped for 500 m over a 15-m gradient in elevation (Bergstrom and Hoffmann, 1991). Differential responses to a larval botfly (*Cuterebra fontinella*) by *T. quadrivittatus* and *T. umbrinus* may be the factor that determines the parapatric boundary in Colorado (Bergstrom, 1992).

In northwestern New Mexico, *T. quadrivittatus* occurs among Ponderosa pines, Douglas firs, and aspens on the upper slopes of higher mountains. *T. dorsalis* is abundant at lower elevations where pinyon and junipers are common. In places where warm, sunny, and protected canyons extend into cooler elevations, the two species occur together. Both occur in oak brush and Ponderosa pine habitats surrounding Mirabal Spring on Mount Taylor, Cibola County. They frequent fallen Ponderosa pines and rock outcrops partly obscured by thickets of oak brush or aspen trees (Hooper, 1941). In the absence of *T. dorsalis*, *T. quadrivittatus* occurs down to the lower edge of woodland and in places even into grassland (Findley, 1969). In most of the mountains of northern New Mexico, *T. quadrivittatus* is sympatric with *T. minimus*, but there usually is some habitat separation. *T. quadrivittatus* is most common in pinyon, juniper, and oak woodland, and in Ponderosa pine and mixed coniferous forests, while *T. minimus* is common in spruce-fir forests or below the range of *T. quadrivittatus* in sage grasslands (Findley, 1987). In the Sandia and Jemez mountains, New Mexico, *T. quadrivittatus* is sympatric with *T. minimus*, however, there was no difference in habitat variables measured for these two congeners (Sullivan, 1985).

Mammals commonly occurring in the same habitat as *T. quadrivittatus* are *Sorex merriami*, *S. monticolus*, *S. nanus*, *S. palustris*, *Ochotona princeps*, *Sylvilagus nuttalli*, *Tamias minimus*, *Tamiasciurus hudsonicus*, *Sciurus aberti*, *Spermophilus lateralis*, *Marmota flaviventris*, *Thomomys talpoides*, *Microtus longicaudus*, *M. mexicanus*, *Zapus*, *Neotoma mexicana*, *Martes americana*, and *Mustela erminea* (Lomolino et al., 1989). In southeastern Colorado, *T. q. quadrivittatus* occurs in the same area as *Notiosorex crawfordii*, *Sylvilagus audubonii*, *Lepus californicus*, *Spermophilus variegatus*, *S. pilosoma*, *S. tridecemlineatus*, *Cynomys ludovicianus*, *Cratogeomys castanops*, *Dipodomys ordii*, *Perognathus flavus*, *Peromyscus leucopus*, *P. truei*, and *Neotoma* (Ribble and Samson, 1987).

Tamias quadrivittatus has tested positive for Colorado tick fever virus (Brown et al., 1989), its fleas have tested positive for plague (*Yersinia pestis*—Karami, 1981), and it dies when artificially infected with plague (Holdenried and Quan, 1956). Ectoparasites include the fleas *Ceratophyllus ciliatus* (Traub et al., 1983), *Epididia stanfordii*, *Catallagia decipiens*, *Anomopsyllus nudatus*—*A. princei* complex (Haas et al., 1973), *Hystrichopsylla dippei*, *Stenistomera alpina* (Traub and Hoff, 1951), *Monopsyllus eumolpi*, *M. wagneri*, *Oropsylla idahoensis*, *Peromyscopsylla hesperomys* (Morlan, 1955), *Orchopeas leucopus* (Link, 1949), and *Megarthroglossus procus* (Tipton et al., 1979). Other parasites include the nematodes *Rictularia coloradensis* and *Warrenius quadrivittati* (Hall, 1916), ticks (Link, 1949), the lice *Hoplopleura arboricola* and *Neohaematopinus pacificus* (Morlan and Hoff, 1957), and larvae of the botfly *C. fontinella* (Bergstrom, 1986).

BEHAVIOR. Like most *Tamias*, *T. quadrivittatus* occurs in greatest abundance during early morning and late afternoon (Cary, 1911). The Colorado chipmunk spends ca. 68% of its activity time on the ground, 13% in shrubs, and 19% in trees (Bergstrom, 1986). *T. quadrivittatus* may be seen moving about rocks and stumps of trees on the sides of canyons or along fences, or feeding in thickets of wild cherries and June berries in canyon bottoms (Cary, 1911). It climbs and obtains part of its food from fruits and seeds of trees. Often *T. quadrivittatus* is observed sitting on stumps and rocks watching or feeding. It may be seen in the tops of bushes or on branches of low trees gathering berries or seeds for food. *T. quadrivittatus* harvests grain by cutting it down, shelling, and tucking it into the cheekpouches until they bulge. Acorns and seeds of other plants also are stored, but storing seeds from grainfields seems to be preferred. The food cache often is dug out by badgers, skunks, foxes,

or other animals. An empty and torn up mass of soft grass fibers ≥ 0.3 m below the surface of the ground and a scattered store of seeds often are found. *T. quadrivittatus* also may play a role in interfering with reforestation by digging up and eating the planted seeds of trees (Bailey, 1931).

In Colorado, *T. quadrivittatus* goes into at least partial hibernation over most of its range, depending on length and severity of the winter. Often, *T. quadrivittatus* arouses during mild winter weather (Cary, 1911), and it has been seen every month in mild winters (Warren, 1942). In New Mexico, *T. quadrivittatus* hibernates or remains in its den during the coldest weather. It does not become excessively fat and the period of hibernation is short. *T. quadrivittatus* continues to be active after light snowfalls and when the weather is frosty or when ice forms to considerable thickness at night. In northern New Mexico, *T. quadrivittatus* is active until early December. After the first deep snow no more are seen during the rest of winter. In more southern localities, activity may continue throughout winter. It is possible that *T. quadrivittatus* does not hibernate at all, only living on its stores of food in well-protected nests (Bailey, 1931).

When the weather is too cold or snow is too deep for foraging, the Colorado chipmunk eats food it has stored in burrows or dens (Bailey, 1931). In autumn, it gathers food and caches it in crevices and under rocks (Cary, 1911). When autumn storing of seeds begins, families break up and each individual stores its winter supply separately and close to its own nest chamber (Bailey, 1931). *T. quadrivittatus* is not known to use arboreal nests (Broadbooks, 1977).

Calls of *T. quadrivittatus* include a chip, trill, chipper, and squeal (Bergstrom and Hoffmann, 1991). Chips commonly are emitted, usually from a promontory (e.g., from the summit of a large rock, tree branch, or tree stump—Bailey, 1931; Cary, 1911) in bouts from a few seconds to 15 min. Chipping displays seldom are given in response to any predator or human intruder. When accipiters make low passes through an area, either no chips are given, or single, scattered, or short bouts of chips are given. Occasionally, *T. quadrivittatus* may conduct chipping bouts of 2–5 min each. Trills sometimes are interjected into bouts of chips. Both chips and trills are emitted by animals in traps. Squeals often are emitted during handling by humans. These sounds are similar to those made by juveniles when distressed, but are made by animals of all ages. When handled, the Colorado chipmunk frequently enters a trance lasting ca. 1 min after being held by the nape. At this time, it is immobile. Chips usually are emitted during flight, but sometimes are difficult to distinguish from trills (Bergstrom and Hoffmann, 1991).

Tamias quadrivittatus vocalizes less frequently in traps than *T. minimus* and *T. umbrinus*. *T. quadrivittatus* squeals at a greater rate when handled, its chips have a distinctive tonal quality in that they are raspy (those of the other two species are clearer), and it has chips that are longer (77.9 ms) and with greater variation (Bergstrom and Hoffmann, 1991). When calling, the tail of *T. quadrivittatus* gently waves (Bailey, 1931). Often, especially in longer bouts of calling, regularly spaced chips are given in synchrony with a tail flick. Tail movements of *T. quadrivittatus* and *T. umbrinus* typically have a horizontal component (a slow, side-to-side sway), whereas those of *T. minimus* typically are vertical (a rapid upward flick—Bergstrom and Hoffmann, 1991).

Social dominance is shown by chasing behavior (Gordon, 1936). *T. quadrivittatus* usually is shy, and when surprised, may take refuge among rocks (Cary, 1911), in hollow logs, in tree tops, or on the opposite side of the nearest tree. At campsites, *T. quadrivittatus* is inquisitive, often becomes tame, and may congregate in large numbers (Bailey, 1931).

GENETICS. *Tamias quadrivittatus* has karyotype B of *Tamias* (Nadler, 1964). The diploid number of chromosomes is 38, including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969). The diploid number may vary from 36 to 38 (Nadler, 1964).

Based on an electrophoretic examination of blood-serum proteins, there are no differences between individuals of different sex, age, or period of captivity (Burgwardt, 1968). Based upon 20 allozymes, *T. quadrivittatus* had an average heterozygosity of 0.0606 and four polymorphic loci (serum transferrin, two loci for red cell phosphoglucose mutase, and 6-phosphoglucose dehydrogenase—Levenson et al., 1985). An examination of 24 allozymes revealed that

21 were monomorphic; glutamate oxalate transaminase, esterase, and peptidase were heterozygous. Average number of alleles per locus was 1.1, the proportion of loci polymorphic per population was 12.5, and average proportion of the 24 loci heterozygous per individual was 0.029 (Sullivan, 1985).

REMARKS. Phenetic analyses of morphologic characters have grouped *T. quadrivittatus* in clusters with *T. cinereicollis*, *T. dorsalis*, *T. palmeri*, *T. panamintinus*, and *T. umbrinus*. Cladistic analyses of electrophoretic data have placed *T. quadrivittatus* with *T. dorsalis*, *T. minimus*, *T. panamintinus*, *T. speciosus*, and *T. ruficaudus* (Levenson et al., 1985; Nadler et al., 1985). Based upon these analyses, Levenson et al. (1985) considered *T. quadrivittatus* to be a member of the *dorsalis* species group with *T. dorsalis*, *T. panamintinus*, and *T. rufus*.

On the basis of a much smaller baculum and average smaller size of body, *T. rufus* is regarded as a species distinct from *T. quadrivittatus* (Patterson, 1984a). Based upon bacular morphology, the population from the Organ Mountains, New Mexico, is considered to be *T. quadrivittatus* rather than *T. canipes* or *T. cinereicollis* (Patterson, 1980). There is no basis for the derivation of *T. canipes* from *T. cinereicollis*. Instead, both species appear to have been derived independently from a northern stock currently represented by *T. quadrivittatus* (Patterson, 1982).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Levenson et al., 1985; Nadler et al., 1969, 1977; Wilson and Reeder, 1993). However, there are indications that *Eutamias* and *Tamias* may be distinct genera, e.g., divergence in the late Miocene (Ellis and Maxson, 1979; Hafner, 1984), differences in pattern of dorsal stripes, structure of the hyoid, chromosomes, dental formulas, bacula (Hoffmeister, 1986), microcomplement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

Tamias is from the Greek *tamias* meaning a storer or distributor. The specific epithet *quadrivittatus* is derived from the Latin *quadrus* meaning fourfold and *vittatus* meaning striped (Jaeger, 1955). Additional common names are larger Colorado chipmunk and qua-mhéu-na of the Taos Indians (Bailey, 1931). Because *T. quadrivittatus* was the first American species of chipmunk to be named, many species of North American chipmunks have a taxonomic history that includes the name *quadrivittatus*; e.g., *T. amoenus*, *T. minimus*, *T. rufus*, *T. speciosus*, and *T. townsendii* (Howell, 1929; Patterson, 1984a).

We thank L. L. Thornton, A. M. Coffman, and other personnel in the Interlibrary Loan Department at Auburn University R. B. Draughon Library for assistance in obtaining articles from other institutions, K. J. Adams at the University of Texas at Austin (University Archives) for providing access to Say (1823), and K. A. Howard for preparing Fig. 3. B. J. Bergstrom, M. K. Causey, M. C. Wooten, and an anonymous reviewer provided helpful comments on an early draft of the manuscript. This is journal article no. 15-923337 of the Alabama Agricultural Experiment Station.

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- Editors of this account were GUY N. CAMERON and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.
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